

# Temperature Effects on Snapping Performance in the Common Snapper *Chelydra serpentina* (Reptilia, Testudines)

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## ABSTRACT

Studies on the effect of temperature on whole-animal performance traits other than locomotion are rare. Here we investigate the effects of temperature on the performance of the turtle feeding apparatus in a defensive context. We measured bite force and the kinematics of snapping in the Common Snapping Turtle (*Chelydra serpentina*) over a wide range of body temperatures. Bite force performance was thermally insensitive over the broad range of temperatures typically experienced by these turtles in nature. In contrast, neck extension (velocity, acceleration, and deceleration) and jaw movements (velocity, acceleration, and deceleration) showed clear temperature dependence with peak acceleration and deceleration capacity increasing with increasing temperatures. Our results regarding the temperature dependence of defensive behavior are reflected by the ecology and overall behavior of this species. These data illustrate the necessity for carefully controlling  $T_b$  when carrying out behavioral and functional studies on turtles as temperature affects the velocity, acceleration, and deceleration of jaw and neck extension movements. More generally, these data add to the limited but increasing number of studies showing that temperature may have important effects on feeding and defensive performance in ectotherms. *J. Exp. Zool.* 315:41–47, 2011. © 2010 Wiley-Liss, Inc.

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Temperature has been shown to have pervasive effects on all levels of biological organization (Huey, '82; Hochachka and Somero, '84). Body temperature ( $T_b$ ) affects nearly all ecological, behavioral, and physiological processes of ectotherms (Huey, '82), and consequently affects the fitness of an organism (Huey and Kingsolver, '89). Body temperature influences speed of locomotion (Van Damme et al., '91; Claussen et al., 2002; Herrel et al., 2007), growth rate (Angilletta and Dunham, 2003), heart rate (Hochscheid et al., 2002), prey capture ability (Wintzer and Motta, 2004), and the response to predators (Weetman et al., '98; Forsman, '99). Because reptiles typically do not generate heat to maintain an optimal  $T_b$ , thermoregulatory behavior is a salient feature of reptile biology (Huey and Slatkin, '76; Huey, '82). There is often an optimal range of temperatures that must be achieved

for effective metabolic function, immunochemical protection, and digestion of food (Anderson and Wilbur, '48; Wright et al., '57; Obbard and Brooks, '79; Hammond et al., '88; Knight et al., '90; Van Damme et al., '91). As a consequence, performance (i.e. the ability of an organism to execute an ecologically relevant task; Huey and Stevenson, '79), which is dependent on

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physiology, is dependent on the thermal environment as well. Previous studies of the thermal dependence of physiological performance have focused on locomotor variables such as maximum velocity, endurance, and exertion capacity (Lailvaux and Irschick, 2007), ingestion (Van Damme et al., '91; Alexander et al., 2001), and food assimilation (Zhang and Ji, 2004).

Although many studies have focused on bite force capacity in vertebrates, these have predominantly focused on comparing head size and bite performance in ecological and behavioral contexts (Herrel, 2001a,b, 2005; Anderson et al., 2008). Interestingly, aggressive behavior appears to be temperature dependent as well (Hertz et al., '82). Biting force capacity, however, is an aspect of defensive behavior that is expected to be less dependent on changes in temperatures in lizards and other ectotherms (Herrel et al., 2007) as previous workers have shown that the force generation capacity of muscle has a low thermal dependence in contrast to activation and relaxation times of muscles, which are strongly dependent on temperature (Bennett, '85; Herrel et al., 2007). Bite force generation is a relevant trait in aggressive interactions (Lailvaux et al., 2004) and in a defensive context (Herrel et al., 2007). Moreover, as bite force may be less dependent on temperature than, for example, locomotor performance, this performance trait may be crucial in species potentially experiencing large temperature fluctuations.

The performance of the cranial system plays a key role in survival of turtles as it is related to both prey capture and defensive capacity. Studies of the thermal sensitivity of such traits may contribute to a greater understanding of how these factors may influence organismal fitness and distributional patterns. Jaw action during food capture has been extensively studied in aquatic turtles from both a functional and an evolutionary perspective (Weisgram, '85; Lauder and Prendergast, '92; Bels et al., '98). However, the thermal dependence of jaw movements in turtles remains largely unstudied (but see Bels et al., 2008). Moreover, it remains unknown to what degree biting performance beyond simple bite force capacity (e.g. the velocity and acceleration of jaw and neck movements) is affected by body temperature. We here describe the relationship between body temperature and biting performance in a turtle that relies on biting in defensive, feeding-related, and aggressive contexts.

The Common Snapping Turtle (*Chelydra serpentina*) is notorious for its aggressive nature. In contrast to other turtle species, it uses snapping as a defense. As it has a reduced carapace, snapping is, in addition to its large body size, its only means of defense. Thus, it is crucial that this behavior is operational within the natural temperature range experienced by this species. However, as this species has a large distributional range and is consequently confronted with a wide range of environmental temperatures (average air temperature: 12–34°C, see Steyermark et al., 2008), understanding the effects of temperature on defensive snapping is crucial (Carr, '69). The Common Snapping Turtle may occupy nearly all types of water

bodies (except marine), ranging from cold, temperate, to near tropical, and may have one of the greatest latitudinal distributions of any turtle (Steyermark et al., 2008), making it a good model to study effects of temperature on performance. We here address the question whether temperature has an effect on bite force, kinematics of snapping, and the willingness to snap in the Common Snapping Turtle (*C. serpentina*). Given that muscle force production, but not contractile velocity, is largely independent of temperature (Bennett, '85) we predict that whereas bite force capacity should be independent of temperature, the kinematics of snapping should be affected. Moreover, the willingness to bite should be independent of temperature if bite force capacity is indeed independent of temperature. A greater understanding of how temperature affects the performance of the jaw system during a defensive context may shed light on the effects of temperature on ecologically relevant capacities of the jaw system in general such as feeding.

## MATERIALS AND METHODS

### Study Species and Housing

The Common Snapping Turtle (*C. serpentina*) is a large (up to 47 cm carapace length), aquatic or semi-aquatic turtle (Ernst et al., '88; Gibbons et al., '88). We made use of four captive animals from a private collection. All animals ranged in carapace length from 23.0 to 26.5 cm (mean =  $24.6 \pm 1.3$ ). The Common Snapping Turtles were maintained in a 350L aquarium (water depth 30 cm) with dechlorinated water and were fed live goldfish (*Carassius auratus*) and worms (*Lumbricus terrestris*) 2–3 times weekly. Animals were held on a photoperiod of approximately 12 hr light and 12 hr darkness. Water was actively filtered (Eheim professional) and aerated (Rena Air 50).

Turtles were kept in a large plastic basin for two days with the selected water temperature during experimental trials and  $T_b$  was checked before each measurement. Between the trials, turtles were returned to their aquaria. For practical reasons (measurement equipment, increased aggressiveness of the turtles) the measurements were conducted out of water. We measured body (cloacal =  $T_b$ ) temperatures to the nearest 0.1°C with a thermocouple connected to a digital thermometer (APPA 51, precision 0.1°C). The preferred body temperature was obtained by warming up the water basin using several aquarium heaters (Rena 150 Watt).

### Bite Force

In vivo bite forces were measured using an isometric Kistler force transducer (type 9311B, range  $\pm 5,000$  N; Kistler Inc., Winterthur, Switzerland) mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5058 A, Kistler Inc.). All the animals were induced to bite on two plates, set at a fixed distance of 3.65 cm (see Herrel et al., 2002). When a turtle was held in front of the bite plates, it typically resulted in forceful, aggressive,

and prolonged biting (Fig. 1). For each animal, bite force measurements were repeated ten times and the point of application of the bite force was standardized across trials. We considered the maximum value across all trials as the maximum bite force for that individual turtle.

In order to circumvent problems associated with habituation, the sequence of trial temperatures was randomized. The turtles were measured at each of the six temperatures, 15, 17.5, 21, 24, 30, and 35°C. These temperatures were chosen to cover a wide range of temperatures within the thermal range of activity (Steyermark et al., 2008). Turtles became unresponsive and refused to bite at temperatures below 15°C and above 35°C.

**Kinematic Analysis**

The turtles were filmed in lateral view at 250Hz using a Redlake Motionscope Digital High-Speed Camera (Cheshire, CT). A background grid of 100 mm squares was used as the scale. We measured the kinematic variables associated with biting (closing of the jaws) and striking (neck movements); and calculated the linear velocity, acceleration, and deceleration of the jaws, and the time needed to close the jaws. Animals were induced to bite a wooden stick covered with a strip of polyurethane foam secured and covered with duck tape. Turtles were induced to snap ten times at each trial temperature and  $T_b$  was checked before each trial. One-hour of rest was provided between subsequent bite sessions and two days of rest between different test temperatures. During this period turtles were held at the desired test temperature. Video recordings were reviewed using Midas Player Software (Redlake, San Diego, CA; version 2.1.7). Lateral images of the animals were digitized and analyzed using Didge (Image Digitizing Software version 2.2.0; Alistair Cullum). Landmarks were placed on the tip of the upper jaw and tip of the lower jaw and the most anterior point of the eye. Gape distance (defined as the distance between the ventral-most point of the anterior surface of the premaxilla and the dorsal-most point of the anterior surface of the mandibular symphysis) was calculated using  $x,y$  coordinates of lower and upper jaw (Fig. 1). To estimate



Figure 1. Head of Common Snapping Turtle, indicating the digitized landmarks.

Table 1. Overview of mean performance measurements of *Chelydra serpentina* under different temperature intervals.

Temperature (°C)	Bite force			Jaw closing			Neck extension		
	Maximum (N)	Velocity (cm/sec)	Time (sec)	Acceleration (cm/sec <sup>2</sup> )	Deceleration (cm/sec <sup>2</sup> )	Time (sec)	Velocity (cm/sec)	Acceleration (cm/sec <sup>2</sup> )	Deceleration (cm/sec <sup>2</sup> )
15	123 ± 7.52	112.02 ± 5.73	4.02 × 10 <sup>-2</sup> ± 2.77 × 10 <sup>-3</sup>	6,406.65 ± 925.33	-6,279.93 ± 612.24	4.02 × 10 <sup>-2</sup> ± 2.77 × 10 <sup>-3</sup>	44.95 ± 9.8	3,571.87 ± 1,056.02	-4,171.25 ± 1,050.32
17.5	126.33 ± 5.36	146.41 ± 5.16	3.21 × 10 <sup>-2</sup> ± 1.09 × 10 <sup>-3</sup>	11,661.97 ± 749.19	-13,743.78 ± 1,323.75	3.21 × 10 <sup>-2</sup> ± 1.09 × 10 <sup>-3</sup>	73.52 ± 11	8,169.97 ± 965.89	-9,115.97 ± 774.11
21	131.75 ± 3.5	133.6 ± 14.36	2.79 × 10 <sup>-2</sup> ± 9.19 × 10 <sup>-4</sup>	13,993.67 ± 1,066.15	-14,207.34 ± 2,365.26	2.79 × 10 <sup>-2</sup> ± 9.19 × 10 <sup>-4</sup>	65.34 ± 7.16	7,475.74 ± 883.48	-9,983.96 ± 862.34
24	124.5 ± 8.87	154.96 ± 7.89	2.83 × 10 <sup>-2</sup> ± 9.63 × 10 <sup>-4</sup>	10,989.41 ± 979.77	-14,153.83 ± 1,291.44	2.83 × 10 <sup>-2</sup> ± 9.63 × 10 <sup>-4</sup>	77.75 ± 9.65	9,009.43 ± 1,032.73	-9,639.80 ± 1,067.27
30	136.5 ± 8.45	157.48 ± 14.95	2.04 × 10 <sup>-2</sup> ± 1.02 × 10 <sup>-3</sup>	11,728.13 ± 2,808.77	-15,586.96 ± 3,516.78	2.04 × 10 <sup>-2</sup> ± 1.02 × 10 <sup>-3</sup>	66.93 ± 10.26	7,033.22 ± 1,373.09	-8,508.13 ± 981.93
34	128 ± 7.51	191.05 ± 6.77	1.91 × 10 <sup>-2</sup> ± 7.35 × 10 <sup>-4</sup>	16,375.79 ± 1,065.99	-20,953.7 ± 2,794.38	1.91 × 10 <sup>-2</sup> ± 7.35 × 10 <sup>-4</sup>	67.47 ± 15.24	7,176.50 ± 1,915.32	-8,416.99 ± 1,653.81

neck movements we used the landmark on the ventral-most point of the anterior surface of the premaxilla relative to a fixed background grid. The raw displacement profiles of the jaws were smoothed using a Butterworth low-pass filter at 50 Hz (Van Wassenbergh et al., 2007). Velocities and accelerations were calculated from the filtered displacement data by taking the first and second derivatives.

In addition to the variables listed above we also subjectively judged the motivation of the animals to snap at different temperatures. We gave scores ranging from 1 to 4, depending on their willingness to snap. Scores were assigned as 1, poor; 2, moderate; 3, good; and 4, excellent (Fig. 4).

To examine the effects of temperature on bite performance, all variables were logarithmically transformed ( $\log_{10}$ ) before analysis. We performed repeated measures analysis of variance (ANOVA) to determine whether performance and kinematic variables differed between the temperatures (Sokal and Rohlf, '81). A  $\chi^2$  test was used to test the willingness to snap under different temperatures. All analyses were performed using SPSS (version 11.5).

## RESULTS

Descriptive values of the performance characteristics are given in Table 1. Bite force is temperature insensitive (Temperature effect, Table 1,  $F_{6,19} = 5.24$ ,  $P = 0.084$ ). Moreover, strike velocity (Temperature effect,  $F_{5,16} = 1.29$ ,  $P = 0.31$ ), and strike acceleration (Temperature effect,  $F_{5,16} = 2.8$ ,  $P = 0.052$ ) were not affected by temperature. We also did not detect differences in the willingness of these turtles to snap at different temperatures (Fig. 4; Fisher Exact test;  $\chi^2 = 8.05$ ,  $P = 0.187$ ).

In contrast, we did find statistically significant differences in velocity (Table 1 and Fig. 2; Temperature effect,  $F_{5,16} = 6.58$ ,  $P = 0.001$ ), acceleration (Fig. 2; Temperature effect,  $F_{5,16} = 6.64$ ,

$P = 0.001$ ), deceleration (Fig. 2; Temperature effect,  $F_{5,16} = 6.96$ ,  $P = 0.001$ ), and the total time (Fig. 3; Temperature effect,  $F_{5,16} = 25.44$ ,  $P < 0.001$ ) of jaw closing. Additionally, neck deceleration was affected by temperature (Temperature effect,  $F_{5,16} = 4.42$ ,  $P = 0.01$ ). Tukey a posteriori tests revealed major differences between the outermost data points (i.e. the highest and lowest temperatures).

## DISCUSSION

In this study, we found values for bite forces in *C. serpentina* comparable with those previously reported for this species (Herrel et al., 2002) and typically greater than the bite forces of most other turtles. As *Chelydra* consumes a lot of hard prey (including

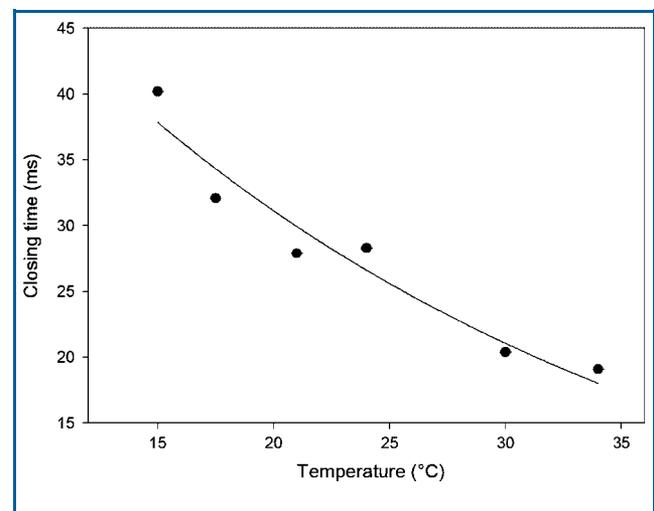


Figure 3. Average time (msec) for jaw-closing under different temperatures (°C).

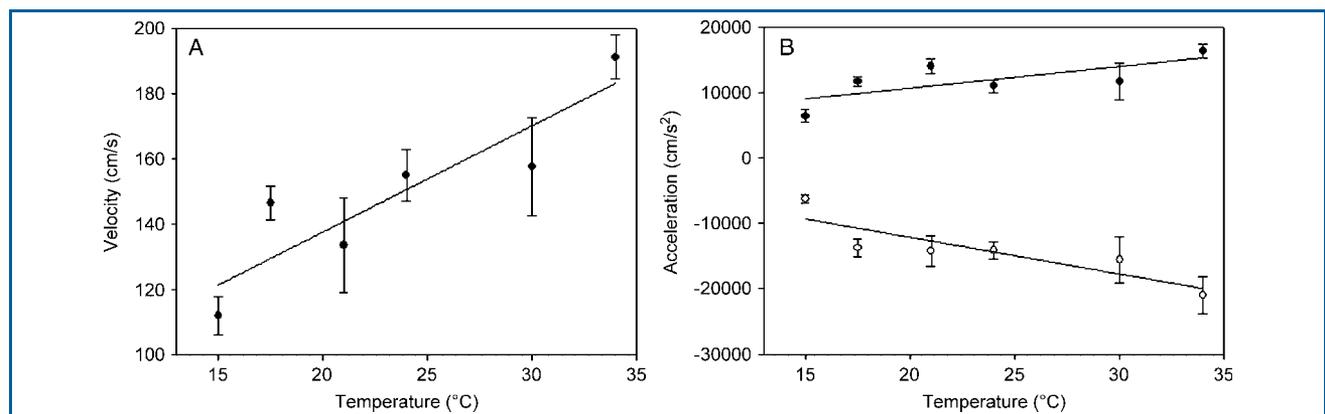


Figure 2. Mean kinematics under different temperatures. Panel A represents acceleration ( $\text{cm}/\text{sec}^2$ ); open circles are acceleration and deceleration. Panel B represents speed of jaw action ( $\text{cm}/\text{sec}$ ), represented by triangles. Circles and triangles denote the mean and standard errors.

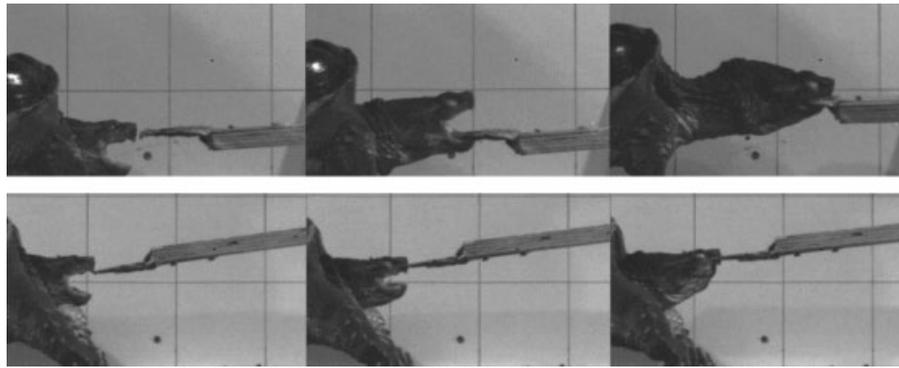


Figure 4. Sequences of strikes in *Chelydra serpentina*. Upper part: Excellent strike (class 4) and lower part: poor strike (class 1).

other turtles, see Carr, '69) requiring large bite forces to be processed, this observation is not surprising. Our results indicate that the aquatic turtle *Chelydra* is unable to snap quickly at lower temperatures, but suggest a constant bite force capacity over a large range of body temperatures. This suggests that although they can effectively defend themselves, they may not be able to capture elusive prey at low body temperatures.

These results are consistent with findings about aquatic and terrestrial locomotor performance in turtles such as burst speed, endurance, and righting response, in which locomotor performance increased with increasing temperatures (Claussen et al., 2002; Elnitsky and Claussen, 2006). We were not able to detect thermal differences in the willingness to snap, clearly indicating its defensive role. The sustained willingness to snap and bite in a defensive context, coupled to the temperature independence of absolute levels of bite force capacity, may allow these animals to effectively defend themselves even at lower temperatures experienced at the Northern limits of their distributional range during the end of the activity season.

Bels et al. (2008) compared gape performance at three temperatures: 24, 28, and 30°C in three specimens of *Trachemys* (Emydidae), *Cuora* (Emydidae), and *Siebenrockiella* (Bataguriidae). They studied the effect of temperature on bite time (i.e. time to contact food) and jaw opening time (i.e. time to maximum gape). Because *Trachemys* bites faster than its Asian relative *Cuora*, Bels et al. (2008) suggested that this might explain the role of feeding performance in the invasive success of *Trachemys* turtles. In the study of Bels et al. (2008) *Siebenrockiella* (Bataguriidae) would not feed at 18°C. Our data suggest a similar unwillingness to snap in *Chelydra* under temperatures below 15°C and above 35°C. Jointly these data suggest that temperature may have an important effect on aggressive interactions in an interspecific or defensive context.

*C. serpentina* is a particularly relevant species in this context as it has a great distributional range and is consequently confronted with a large range of environmental temperatures including large

seasonal fluctuations at northern latitudes. Interestingly, ecological data suggest that at the northernmost limit of the distribution of the Common Snapping Turtle, populations have the highest incidence of atmospheric basking which may be used to compensate for the lower environmental temperatures (Obbard and Brooks, '79). The reduction in jaw velocity and acceleration with decreasing temperature has consequences on the ability of these turtles to catch mobile prey and increased basking may allow animals to minimize these effects at higher latitudes. Lauder and Prendergast ('92) showed that *Chelydra* relies heavily upon the acceleration of the head when catching prey. The movement of the head and neck toward the prey during a feeding event produces a hydrodynamic pressure gradient that can be detected by the Mauthner neurons of the fish and may result in a startle escape response (Bramble, '78; Lauder and Prendergast, '92), thus emphasizing the importance of a rapid acceleration of the head toward the prey. Since *Chelydra* naturally feeds on many different types of prey items (Carr, '69; Ernst and Barbour, '72; Hammer, '75; Pritchard, '79) that vary greatly in agility and size, seasonal shifts due to differences in the performance of the feeding apparatus probably exist in the wild. Based on our data we suggest that capturing active prey at low temperatures is nearly impossible for *Chelydra*, which is consequently forced to hibernate.

One puzzling aspects of our results was the lack of an effect of temperature on neck extension velocity and acceleration despite the strong effects on deceleration and jaw closing velocity, acceleration, and deceleration. Although it currently remains unclear why this might be the case, we suggest that animals may rely on some form of elastic energy recoil to rapidly propel the head and neck forward during snapping. Not only would this explain the observed lack of a temperature effect on extension velocity and acceleration, it would also simplify the control of neck extension. Deceleration, in contrast, is likely governed by direct muscular action and is thus affected by temperature. These results are similar to recently published finding on the temperature insensitive nature of ballistic tongue projection,

but not retraction, in chameleons (Anderson and Deban, 2010). Further studies explicitly testing for the presence of elastic recoil mechanisms are needed to test this hypothesis, however.

The results obtained by our experiments, which were conducted in the air for practical reasons, have their obvious limits and consequences. Given the higher density of water compared to air, we can expect that the reached velocities measured in this study or higher than those performed by animals in their natural aquatic environment. However, performance will be affected to a similar degree relative to temperature, and consequently would not invalidate our conclusions.

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